# Distribution of clonal and non-clonal wetland plants at Clydebank Morass, Gippsland Lakes, in relation to elevation and salinity gradients

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## Abstract

A review of the published literature suggested that plants with a clonal growth habit dominated the vegetation of wetlands in many parts of the world. To test whether this pattern held in Australia, the distribution of plants with clonal and non-clonal growth habits was examined in Clydebank Morass, a brackish-water wetland of the Gippsland Lakes in south-eastern Victoria. Nineteen of the twenty species of aquatic or semi-aquatic plants present in the wetland were clonal. In terms of both species number and percentage cover, clonal plants dominated the vegetation in wet and intermittently damp parts of the Morass whereas non-clonal plants were progressively more common as elevations increased. This elevational effect was due more to changes in soil moisture content than in soil salinity. These results not only confirmed the prediction that clonal plants were the dominant growth habit in the wetland but were consistent with predictions made in the 1960s as to likely vegetation changes as the Gippsland Lakes became progressively salinised. Understanding the dominance of wetlands by clonal plants has implications for assessments of plant fitness and the maintenance of plant biodiversity and habitat heterogeneity; it is central also to improving the success with which degraded wetlands are rehabilitated. (*The Victorian Naturalist* **125** (1), 2008, 11-18)

## Introduction

Clonal plants are those that can reproduce asexually and spread as a population of semi-independent parts of what was originally a single seedling (Harper 1977). Clonal growth and vegetative reproduction may occur in many ways, including the production of rhizomes, stolons, tubers, turions and plantlets, fragmentation of the plant body, and node rooting. Many of these features are evident in well-known and widely distributed wetland and aquatic plants – for example willows *Salix* spp., Eel Grass *Vallisneria* spp., Common Reed *Phragmites australis* and Cumbungi *Typha* spp. Indeed, a number of international studies have indicated that wetlands are often dominated by clonal plants, which can reproduce vegetatively as well as sexually by seed when environmental conditions permit (Mühlberg 1982; Cook 1990; Grace 1993; Oborny and Bartha 1995; van Groenendael *et al.* 1997; Crow and Barre Hellquist 2000). For example, 61% and 68% of the aquatic or wetland plant species in North Carolina and Florida, respectively, are clonal (Beal 1977; Tarver *et al.* 1978). Spencer Jones and Wade (1986) reported that 88% of vascular aquatic plant species in the British Isles are clonal. Clonal plants also have been shown to dominate the floristics of wetlands in Central Europe (Klimeš *et al.* 1997; L. Klimeš, pers. comm. 2005) and China (Song and Dong 2002).

There have been no comparable studies undertaken to examine the importance of clonality in the vegetation of wetlands of temperate south-eastern Australia, but a review of plant descriptions in the three most important monographs on Australian aquatic and wetlands plants in this region – Aston (1977), Romanowski (1998) and Sainty and Jacobs (2003) – indicated that 288 of the 450 described taxa (64%) were clonal and capable of vegetative reproduction. The ratio of approximately 2:1 for clonal to non-clonal aquatic plants was consistent across all three references: 65% in Aston (1977), 61% in Romanowski (1998) and 71% in Sainty and Jacobs (2003). This result would suggest that Australian wetlands, like wetlands in the Northern Hemisphere, are likely to be dominated by clonal plants. Nevertheless, to our knowledge there have been no studies that have attempted empirically to quantify the incidence of clonality – either floristically or in terms of cover or abun-

dance – in an Australian wetland. Moreover, it is unclear even from overseas studies as to what environmental factors are most important in controlling the relative distributions of clonal and non-clonal plants in wetlands.

The research reported in this paper had three aims. The first was to test the hypothesis that clonal plants dominated the aquatic and semi-aquatic vegetation in Clydebank Morass, a brackish-water wetland of the Gippsland Lakes in eastern Victoria. This question was addressed by undertaking vegetation surveys at two contrasting times of year to quantify the relative incidence of clonality in the wetland's aquatic and semi-aquatic vegetation. The second aim was to determine whether the distributions of clonal and non-clonal plant species varied with environmental conditions, especially elevation and soil water content and salinity. The third aim was to use these data on floristics, vegetation cover and environmental conditions to address a number of predictions made in the 1960s as to the likely historical trajectory of plant communities in wetlands that fringe the Gippsland Lakes, with particular reference to increasing salinity. In a series of pioneering papers by ECF Bird in the 1960s (Bird 1961, 1962, 1966), it was predicted that wetlands and fringing vegetation along the Gippsland Lakes would be affected by increasing salinity arising from the artificial opening at Lakes Entrance. Bird (1966) specifically raised the possibility that inexorably increasing salinity would cause the replacement of reed swamp (Common Reed *Phragmites australis*, then known as *P. communis*) by swamp scrub (Swamp Paperbark *Melaleuca ericifolia*) and eventually swamp scrub by even more salt-tolerant salt marsh communities.

## Methods
### Field site
Clydebank Morass (38°02'50"S, 147°14'00"E) is a shallow ($z_{max}$ = 1-2 m), brackish-water wetland of about 1420 hectares in Gippsland, Victoria. It is one of a chain of Ramsar-listed, brackish-water wetlands along the perimeter of Lake Wellington, the westernmost waterbody of the Gippsland Lakes. Clydebank Morass is a State Game Reserve, managed primarily

for waterbird breeding and hunting and habitat values. The wetland has been connected permanently to Lake Wellington since about 1990, when high water levels in the lake breached the low-lying boundary between the Morass and Lake Wellington.

### Vegetation surveys
Floristic surveys were undertaken in late summer (March 2004) and winter (June 2004) to quantify the relative proportions of clonal and non-clonal species. These two survey periods were chosen to maximise the number of plant species identified in the wetland, within the constraints of the time available for field-based assessments. To determine whether the ratio of clonal to non-clonal taxa varied with elevation, 20 belt transects (50 cm wide) were run in July 2004 from the water-line to the most elevated level where terrestrial vegetation bordered the Morass. Transects varied in length from 50 to 100 m and were divided into contiguous 1 m long quadrats. Transects were positioned systematically rather than randomly because systematic samples are particularly well-suited to detecting vegetation changes along environmental gradients and, in such cases, random sampling would generate an arbitrary set of values for species abundance (Kershaw 1973).

Plant cover for vascular plant species in each quadrat was estimated using the Braun-Blanquet scale (0 = 1-5% cover; 1 = 5-10%; 2 = 10-25%; 3 = 25-50%; 4 = 50-75%; and 5 = 75-100%). An inclinometer was used to estimate transect elevations: elevations are given in terms of vertical height above the water level and not with reference to the Australian Height Datum. This decision was necessitated by the lack of survey data or a digital elevation model for the site. Using known measurements of transect lengths and differences in elevation (calculated from inclinometer readings), each of the 20 transect gradients was broken into 0.25 m elevations to allow the zonation width of different taxa to be mapped in terms of elevation above the shoreline. Plant nomenclature follows that of Ross and Walsh (2003).

### Soil characteristics
Soil cores were taken in September 2004 to determine whether there were consistent variations in soil water or salt contents

along the elevational gradients or from zones with contrasting vegetation along a single transect. Three replicate soil cores (5 cm diameter x 10 cm deep) were taken at each quadrat; in total 228 cores from 76 different quadrats were analysed. Soils were sampled to only 10 cm because the species present, even Swamp Paperbark, are quite shallow rooted. Soil cores were oven dried at 105° C to determine moisture contents (MC%, expressed as a percentage of dry-soil weight). To determine salt contents, subsamples were ground with a mortar and pestle, made into slurries (1:5 soil:water), then shaken by inversion for one hour at 25° C (Rayment and Higginson 1992). The temperature-adjusted electrical conductivity of the slurries was converted to salt concentrations (mg L⁻¹) using a conversion factor of 0.6 then tabulated in units of g L⁻¹ of soil pore water.

### Results

*Relative proportions of clonal and non-clonal species*

Ninety plant species from 31 plant families were identified during the two floristic surveys. Exactly one half of the species present were clonal, though this figure increased to 59% when only native taxa were considered (Table 1). Native species accounted for 64% of the species and non-natives 36%; the non-natives were mostly introduced annuals. Guerilla and phalanx clonal growth habits (*sensu* Lovett-Doust 1981) were both well represented at 53 and 47%, respectively. Clonal plants with a guerilla growth habit tend to have long stolons or rhizomes, which allow them to penetrate deeply into new habitats. In contrast, plants with the phalanx growth form tend to have short stolons or rhizomes and colonise new habitats on a broad front, the metaphor reflecting a massed body of infantry drawn up in close order and advancing slowly into new areas. Of the 90 species present in the morass, only 20 were classified as aquatic or wetland plants (Table 2). The definition of aquatic plants was fairly broad and followed the descriptions given by Best (1988) and Sainty and Jacobs (2003). This definition allows for the accommodation of woody tree species, such as Swamp Paperbark and willows, as well as herbaceous taxa.

**Table 1.** Incidence of clonality in plants at Clydebank Morass, Gippsland Lakes, south-eastern Victoria.

| Characteristic | No of species | % |
|---|---|---|
| Total number of plant species | 90 | 100 |
| Native species | 58/90 | 64 |
| Exotic species | 32/90 | 36 |
| Clonal species | 45/90 | 50 |
| Native clonal species | 34/58 | 59 |
| Putative guerilla growth habit | 24/45 | 53 |
| Putative phalanx growth habit | 21/45 | 47 |
| Aquatic species | 20/90 | 22 |
| Clonal aquatic species | 19/20 | 95 |

Of the 20 species found in aquatic or semi-aquatic environments in Clydebank Morass, 19 were easily classified as clonal. The one remaining species, Greater Sea-spurrey *Spergularia media* was an exotic native to Europe and North America, where it typically grows as a perennial above the water-line. At this study site, however, Greater Sea-spurrey was found at the water-line and displayed a growth and senescence cycle typical of an annual species. As there was no evidence of node rooting or other asexual growth, Greater Sea-spurrey was classified as non-clonal. Accordingly, 95% of the wetland plants present in Clydebank Morass were unambiguously clonal.

*Variations with elevation and soil salinity*

Clonal species completely dominated the vegetation of Clydebank Morass at lower elevations, and the proportion of clonal species declined consistently with increasing elevation (Fig. 1). Clonal species accounted for more than 70% of the total number of species in the first metre of vertical elevation and approximately 50% of species up to an elevation of 2.5 m. At elevations greater than 3 m from the water-line, the number of clonal taxa declined to around 20% and remained at this value until the highest elevation (6 m) examined in this study. The dominance of clonal taxa was evident not only in terms of floristic criteria (Fig. 1) but also in terms of percentage cover: up to an elevation of about 2 m, clonal plants provided a cover of >75% (Fig. 2).

The distribution of individual plant taxa also varied with elevation. Common Reed

**Table 2.** Range of clonal attributes possessed by wetland plants at Clydebank Morass, Gippsland Lakes, south-eastern Victoria. * indicates an exotic species. [SM]indicates a species identified as a salt-marsh plant by Bridgewater *et al* (1981).

| Family | Species name | Common name | Clonal attribute |
|---|---|---|---|
| Aizoaceae | *Disphyma crassifolium*[SM] | Purple Noon-flower | Node roots |
| Asteraceae | *Cotula coronopifolia*[SM] | Water-buttons | Node roots |
| | *Leptinella longipes* | Coast Cotula | Stolons |
| Caryophyllaceae | *Spergularia media*\* | Greater Sea-spurrey | Non-clonal |
| Chenopodiaceae | *Sarcocornia quinqueflora*[SM] | Beaded Glasswort | Stolons |
| Cyperaceae | *Baumea arthrophylla* | Soft Twigrush | Rhizomes |
| | *Bolboschoenus caldwellii* | Sea Club-rush | Rhizomes |
| | *Eleocharis minuta*\* | Variable Spike-rush | Stolon or rhizomes |
| | *Eleocharis pusilla* | Small Spike-rush | Rhizomes |
| | *Isolepis nodosa*[SM] | Knobby Club-rush | Rhizomes |
| Goodeniaceae | *Selliera radicans*[SM] | Shiny Swamp-mat | Node roots |
| Juncaceae | *Juncus pallidus* | Pale Rush | Rhizomes |
| | *Juncus kraussii* subsp. *australiensis*[SM] | Sea Rush | Rhizomes |
| Juncaginaceae | *Triglochin striatum*[SM] | Streaked Arrow-grass | Rhizomes |
| | *Triglochin procerum* | Water-ribbons | Tubers and rhizomes |
| Myrtaceae | *Melaleuca ericifolia* | Swamp Paperbark | Suckers and rhizomes |
| Poaceae | *Phalaris aquatica*\* | Toowoomba Canary-grass | Rhizomes |
| | *Phragmites australis* | Common Reed (Djarg) | Rhizomes |
| Scrophulariaceae | *Mimulus repens* | Creeping Monkey-flower | Node roots |
| Typhaceae | *Typha domingensis* | Cumbungi, Bulrush | Rhizomes |

*Phragmites australis*, for example, was present only at the wettest end of elevational gradients, up to about 0.5 m elevation (data not shown). In contrast, a second set of plant taxa, consisting of Sea Rush *Juncus kraussii*, Purple Noon-flower *Disphyma crassifolium*, Swamp Paperbark and Blue Tussock-grass *Poa poiformis*, was present in the ephemeral ecotonal zone with mean elevations extending to approximately 1.25 m above the water level. Vegetation in the highest, and driest, zone consisted of Australian Salt-grass *Distichlis distichophylla* and exotic annual species, mostly pasture escapes.

This pattern of plant distributions was related more to variations in soil moisture content than the salinity of the soil pore water. There was a gradual decrease in the mean soil moisture content from the wettest zone colonised by Common Reed (93% w/w soil-moisture content) and Sea Rush (85%) to values of 61% in soils beneath Blue Tussock-grass stands and 50% under Purple Noon-flower. A one-way analysis of variance (ANOVA) showed a significant difference ($F_{5,74} = 9.138$, $P < 0.0001$) in mean soil-moisture content across this gradient. In contrast to the results obtained with soil-moisture contents, average soil salinities were not sig-

nificantly different (one-way ANOVA: $F_{5,74} = 1.474$, $P > 0.05$) with elevation across the transects. The highest average soil salinity was recorded beneath Swamp Paperbark (21 g L⁻¹) in the peaty ephemeral ecotone, whereas the lowest average soil salinity (17 g L⁻¹) was recorded beneath Common Reed, at the wettest end of the gradient. Because of the nature of the conversion from electrical conductivity to salinity, these salt concentrations should be regarded as only approximate.

**Discussion**

Our surveys at Clydebank Morass indicated that 19 of the 20 aquatic or semi-aquatic species present were clonal, and the single remaining species that was not clonal, Greater Sea-spurrey, was an exotic native to Europe and North America, where it typically grows as a perennial above the water-line. This empirical analysis confirms the pattern presented in the main taxonomic monographs covering wetland and aquatic plants in southern Australia (Aston 1977; Romanowski 1998; Sainty and Jacobs 2003), as well as a large number of comparable studies undertaken on the incidence of clonality in wetlands in Europe, the Americas and Asia (see Introduction).
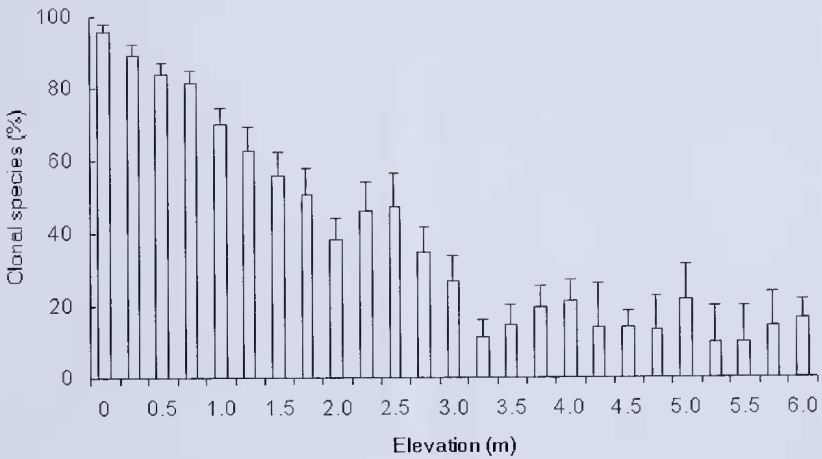
**Fig. 1.** Percentage of clonal plants, as a proportion of total species, in relation to elevation at Clydebank Morass, Gippsland Lakes, south-eastern Victoria. Means and standard errors are shown, n = 20.
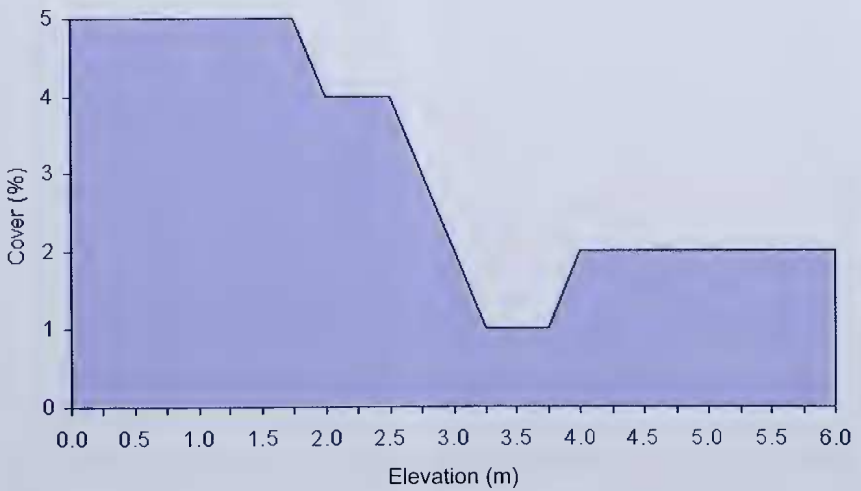


**Fig. 2.** Percentage cover of clonal plant species along 10 elevational gradients at Clydebank Morass, Gippsland Lakes, south-eastern Victoria. The Braun-Blanquet scale is used as the index of cover on the y-axis (0 = 1-5 % cover; 1 = 5-10 %; 2 = 10-25 %; 3 = 25-50 %; 4 = 50-75 %; and 5 = 75-100 %).

It seems that Clydebank Morass is similar to wetlands in other parts of the world in that its aquatic and semi-aquatic vegetation is overwhelmingly clonal. The dominance of clonal plants has a number of important implications for the understanding and rehabilitation of wetland vegetation. First, it has implications for assessing plant fitness. The occurrence of seeds is commonly used as a measure of fitness for plants, as seed production through outcrossing ensures genetic recombination and creates a diverse and resilient gene pool (Eriksson 1997). Although fitness is traditionally calculated by forecasting the expected seed output of a plant over its lifetime, estimating the lifetime seed production for clonal plants can be very difficult as these plants are potentially immortal and may produce innumerable offspring in the form of clonal propagules and ramets, as well as seeds (Wikberg 1995; Santamaría 2002). Indeed, Pan and Price (2002) argued that an emphasis on seed production has meant that clonal growth has been ignored as a critical component of plant fitness.

Botanists have traditionally seen clonal growth ability as an adaptation to complement the dispersal of seeds (Grace 1993). There are a number of reasons indicating that this view should be reversed when wetland plants are considered, and that the obverse view – that sexual reproduction plays the complementary role to vegetative reproduction – should be erected in its place. In wetlands, recruitment events from seed are irregular and highly unpredictable and seed germination is often dictated by subtle changes in hydrological conditions (Brock and Britton 1995; Rea and Ganf 1994; George *et al.* 2005; Capone and Brock 2006). This means that conditions suitable for sexual recruitment may occur at relatively few times of the year or, in the case of wetlands with variable hydrological regimes, only in a few years every couple of decades. Moreover, the seeds of even dominant wetland plants may be short-lived and this can prevent the formation of a soil seed bank; such a pattern has been demonstrated recently for Lignum *Muehlenbeckia florulenta* by Chong and Walker (2005). In contrast to sexual reproduction, the period suitable for vegetative growth and propagation by wetland plants is

not restricted to a single season or rare time of year having the requisite water regime. Furthermore, as seed or diaspore production is often a function of biomass, long-term persistence through clonal offspring offers a greater probability of continual seed output, so that viable seed will be present within the wetland system if suitable conditions for germination do occur.

Second, the ubiquity of the clonal growth habit has implications for the production and maintenance of habitat diversity in brackish-water wetlands. Large clonal plants, such as Swamp Paperbark, that grow mostly at the lower elevations of the Morass provide more structural and topographical complexity in the landscape than do non-clonal species. At high elevations, structural complexity may be driven largely by season, as temporary gaps are created in the vegetation with the rapid germination, maturation and death of annual species. In contrast, at lower elevations tall phalanx species such as Common Reed, Sea Rush and Swamp Paperbark border one another and are often carpeted beneath by low-growing guerilla species, such as Streaked Arrow-grass *Triglochin striatum,* Shiny Swamp-mat *Selliera radicans,* Creeping Monkey-flower *Mimulus repens* and Purple Noon-flower. The combination of tall phalanx and short guerilla clonal architecture creates a rich mosaic of structure and microtopographical relief.

Finally, the prevalence of clonality has implications for wetland rehabilitation. Seed banks feature prominently in the scientific literature on wetland revegetation and rehabilitation (e.g. Brock and Casanova 2000). 1f, however, many wetland plants recruit, disperse and colonise new areas primarily by vegetative means, wetland managers will have to reconsider the strategies for rehabilitating degraded wetland sites. Three issues seem most important and their resolution may help redress the general failure of wetland rehabilitation in southern Australia reported by de Jong (1997). First, seed may not be the most appropriate mechanism for re-introducing plants into degraded sites: Chambers *et al.* (1995) noted that vegetative recolonisation (e.g. with rhizomes) was the best form of propagation for a wide range of important wetland plants in

south-western Australia, including Jointed Twig-rush *Baumea articulata*, Bare Twig-rush *Baumea juncea*, Pithy Sword-sedge *Lepidosperma longitudinale* and River Club-sedge *Schoenoplectus validus*. Second, the spatial heterogeneity created by large clonal plants may provide opportunities for improving the success of revegetation trials. In earlier field trials the survival of Swamp Paperbark tubestock was improved markedly by planting seedlings into raised hummocks of Water Couch *Paspalum distichum* (Raulings *et al.* 2007). This experimental finding is consistent with field observations that Swamp Paperbark seedlings and juveniles occur mostly on hummocks that offer respite against the stressful combination of waterlogging, salinity and soil acidity occurring in surrounding sediments. Third, the incidence of clonality may force a re-assessment of the number of plants that need to be introduced per unit area of wet-land during revegetation trials. Taking a lead from terrestrial precedents, revegetation trials in wetlands commonly involve planting on close (e.g. 1 m) centres. Since many wetland plants are not only clonal but have short-lived seed (e.g. willows: Sainty and Jacobs 2003; Lignum: Chong and Walker 2005), most of the plants of a given species in a wetland were probably derived from one or few individuals. It may be more appropriate to plant large, long-lived clonal species at far lower densities than is the current common practice and let them develop into discrete but extensive stands over the subsequent decades. This recommendation is, however, not to underestimate the importance of the prodigious amounts of seed that can be produced by some wetland taxa, e.g. *Typha* spp., and the problems this causes for the spread of unwanted species into newly constructed or rehabilitated wetlands.

As well as these implications that are probably widely applicable across south-eastern Australian wetlands, the research findings throw light also on the predictions made over 40 years ago by ECF Bird (1961, 1962, 1966) for fringing and wet-land vegetation of the Gippsland Lakes. When the Gippsland region was first settled by Europeans in the 1840s, the Gippsland Lakes were linked with the Southern Ocean by a shifting and intermittent outlet through the sand barriers between Cunninghame and Red Bluff at the easterly part of Lake King. Although they would open to the sea during large floods, to improve navigability an artificial entrance was cut to the ocean in 1889 at Lakes Entrance, about 5 km from the natural entrance. It is believed that a major consequence of opening the artificial entrance has been to increase the salinity of the Gippsland Lakes, which previously were relatively fresh, being fed by the rivers flowing into Lakes Wellington and King and having only an intermittent linkage with the ocean. Bird (1966) predicted that, because of this progressive and inexorable increase in salinity, the fringing vegetation of the Gippsland Lakes would change as salt-intolerant taxa, such as Common Reed, were replaced by taxa tolerant of the higher salinities, such as Swamp Paperbark and, ultimately, salt marsh species. The findings of our study indicate not only that soils in Clydebank Morass were highly saline (17-21 g $L^{-1}$ at the times of sampling in 2004) but that taxa typical of salt marsh communities were abundant in the wetland. Table 2 identifies those species present in the Morass that were listed in the monograph on salt marshes of southern Australia by Bridgewater *et al.* (1981): it is obvious that a large number of the taxa present in 2004 were, indeed, salt-tolerant salt marsh representatives. Thus the data presented here are consistent with the historical trajectory predicted for fringing and wetland vegetation along the shores of the Gippsland Lakes by Bird (1966). Further historical analysis is required to determine whether these taxa were present before salinities in the Gippsland Lakes apparently commenced their recent increase.

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